STRUCTURE OF NEARSHORE FISH ASSEMBLAGES IN RELATION TO VARYING LEVELS OF HABITAT COMPLEXITY

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ABSTRACT

Complex kelp and rocky habitats can be beneficial to fishes, however, their use of these habitats is poorly understood in northern latitudes. This study examined nearshore kelp habitats to examine the potential effects of kelp density and substrate topography on nearshore fish communities in Kachemak Bay, Alaska. Fish were collected from multiple sand, understory kelp, and understory and canopy kelp sites, along with kelp and substrate complexity measurements. Standard Monitoring Units for the Recruitment of Fish (SMURFs), light traps, shrimp pots, and SCUBA visual surveys were all employed in these collections. Relative fish abundance and community composition varied temporally in all habitats. The dominant fish families were gadids, pleuronectids, hexagrammids, and sebastids. Habitat use differed significantly temporally and spatially in relation to size class. These differences were family specific. Community analysis of the dominant fish families showed that different habitat complexities supported distinct fish assemblages. Low complexity sand habitats were particularly important for juvenile pleuronectids in this region and complex nearshore kelp habitats may be essential fish habitat for juvenile Pacific cod. Although these high complexity nearshore environments may be challenging to sample, they support large fish assemblages and may be essential to a variety of fish families and species.

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INTRODUCTION

Habitat structural complexity can influence fish abundance and diversity (Bell & Galzin 1984, Roberts & Ormond 1987, Willis & Anderson 2003). In nearshore waters, habitat complexity is defined by substrate topography and the added structure of macrophytes. Substrate topography can be attributed to variation in the seafloor itself (sand, bedrock, etc.) or debris on the seafloor (boulders, cobbles, etc.) with increasing complexity coming from increased irregularities in the substrate, i.e. cracks in bedrock or spaces between boulders. Macrophytes are macroalgae, such as canopy forming and understory kelps, and vascular plants such as seagrasses and mangroves. Typically, habitats that contain complex structure support a higher abundance and diversity of fishes. Increasingly complex habitats may influence predator prey interactions (Hixon & Menge 1991, Hixon & Beets 1993, Warfe & Barmuta 2004), reduce water flow (Jackson & Winant 1983, Garcia-Charton & Perez-Ruzafa 1998), and serve as areas for feeding, reproduction, and recruitment (Sale 1991, 1999, Steele 1997, Aburto-Oropeza & Balart 2001). Larval fish may settle in structurally complex habitats due to increased microhabitats (Almany 2004a), which could lead to a non-random distribution of juveniles and subsequently influence adult distribution (Almany 2004b). Post-settlement juvenile predation also may be reduced in areas of increased structural complexity (Beukers & Jones 1997), ultimately impacting adult fish distributions.

Substrate topography in habitats such as rock and coral reefs has been shown to influence fish distribution and abundance (Jones 1988, Hixon & Menge 1991, Hixon & Beets 1993). The main mechanism thought to be responsible for this is a reduction in

predation due to the increased amount of refuge available to prey species (Hixon & Beets 1993, Caley & St. John 1996, Almany 2004a). Increased available refuge due to enhanced substrate topography also has been shown to reduce competition for space (Hixon & Menge 1991, Almany 2004b) and add niche dimensionality (MacArthur & Levins 1967).

In many aquatic systems such as lakes, lowland rivers, estuaries, and nearshore marine habitats, structural complexity also can be provided by macrophytes (Heck & Crowder 1991). For example, seagrass habitats may be essential to fish because of the structural refuge they provide (Baelde 1990, Gotceitas et al. 1997, Heck et al. 2003). Likewise, kelp beds are important to fish communities for a variety of reasons, depending on fish species, age, and the type of macroalgal cover. Fish use kelp beds as spawning and mating grounds (Haegele et al. 1981, Hay 1985, Merrill 1989), nursery grounds (Ebeling & Laur 1985, Carr 1989, Love et al. 1991, Levin 1994), feeding grounds (Hobson & Chess 1976, Schmitt & Holbrook 1985, Singer 1985), refuge from predators (Schmitt & Holbrook 1985, Carr 1992, Gotceitas & Brown 1993, Gotceitas et al. 1995), and shelter from currents (Jackson & Winant 1983).

The increased structure provided by macrophytes is particularly important for newly settled recruits and juvenile fishes and may provide protection from predation. Kelps are macrophytes that are capable of increasing the structure available to early life stages of fishes. Recruits and juveniles have a lower mortality rate in the presence of kelp cover (Savino & Stein 1989), and predators, despite increased abundance of prey items, have a lower catch per unit effort in kelp beds (Anderson 1984). Experimental removal of

canopy kelp in the Gulf of Maine increased the overall cover of understory algal assemblages, which resulted in a significant increase in fish recruit density (Levin 1993). In addition to protection provided by kelp, vascular plants and understory algae close to the substrate are also important macrophytes (Hartney 1996). Juvenile fish may shift from areas of low understory algal density to areas of high understory algal density in the presence of a predator (Holbrook & Schmitt 1988). The differences identified in inter-annual success of kelp and understory algae may ultimately affect survivorship of associated juvenile and adult fish in different ways.

Kelp beds in Alaska are structurally very different than kelp beds elsewhere. The dominant canopy kelps in Alaska include the annual bull kelp, *Nereocystis luetkeana,* and the annual ribbon kelp, *Alaria fistulosa*. *Nereocystis luetkeana*, which is only present during summer months, has a stipe through the mid-water and blades only at the surface. However some mid-water structure is provided by juvenile *N. luetkeana* individuals as they grow toward the surface. While *A. fistulosa* is the primary canopy-forming kelp in the Aleutians, *N. luetkeana* dominates most of Southcentral Alaska. Because Alaska is dominated by annual kelps, there is little to no mid-water structure to act as fish refuge in winter months. Understory species, including *Laminaria* spp., *Saccharina* spp., *Agarum clathratum*, *Costaria costata*, and *Cymathaere triplicate*, typically lie prostrate on the substrate because they are lacking a woody stipe. In contrast, in California, kelp beds are comprised primarily of perennial species, which results in kelp cover throughout the year. These perennial species include the canopy forming giant kelp, *Macrocystis pyrifera,* and the large understory species *Pterygophora californica* and *Eisenia arborea*, which stand

erect above the substrate because of their woody stipes. *Macrocystis pyrifera* also has blades along the stipe that provide structure throughout the water column. The differences in physical structure and seasonal variability between Alaskan kelp beds and lower latitudinal regions may have different effects on the fish communities in these structurally distinct habitats.

The knowledge gained from most studies examining the effects of habitat complexity on fish communities is not applicable in Alaskan waters. Many studies examining the effects of habitat complexity on fish are from tropical regions where coral is the primary component increasing complexity (Roberts & Ormond 1987, Willis & Anderson 2003, Almany 2004b). In general, much less is known about the effects of the increased complexity afforded by rocky kelp habitats on temperate fish populations. The limited work that has been done examining the effects of kelp habitats on fish populations either comes from lower latitudes (Bodkin 1988, Anderson 1994, Carr 1991, Angel & Ojeda 2001) or only examines adult fishes (Hegwer 2003, Hamilton 2004). Due to differences in fish and kelp communities between Alaska and the lower latitude regions of the world, examinations of habitat complexity on fish distribution may not hold true in Alaskan waters.

This study examined the effects of substrate complexity and canopy and understory kelp density on the abundance and distribution of the nearshore fish community in Kachemak Bay, Alaska. Multiple gear types were used in habitats of varying structural complexity to address three hypotheses: (a) increasingly complex habitats will have higher abundances of both juvenile and adult fishes, (b) habitat

complexity will have different effects on various fish families, and (c) fish communities within habitats of similar complexity will be more alike than those of differing complexity.

MATERIALS AND METHODS

Site

This study was conducted from June 2005 to September 2006 in Kachemak Bay, Alaska (Fig. 1). Kachemak Bay is located on the southern tip of the Kenai Peninsula (59°33'25"N 151°35'50"W) and drains into the Gulf of Alaska by way of Cook Inlet. Kachemak Bay is comprised of both marine and estuarine environments. The head of the bay is estuarine, having a low salinity due to an influx of glacial runoff fed by seven glaciers and the Fox River. The mouth of the bay is strongly influenced by both deepwater and surface currents from the Gulf of Alaska (Hamilton 2004, Baird & Pegau 2006).

Nine sites were selected along the southern shore of the bay based on water depth, substrate topography, and macrophyte density (Fig. 1). Three of the most complex replicate sites had irregular substrate topography in addition to understory and canopy kelp species (canopy sites), three replicate sites had irregular substrate topography amid understory kelp species, with no canopy kelp species (understory sites), and three of the least complex replicate sites were sandy, with low substrate topography, and no macroalgae (sand sites) (Fig. 1). All sites were approximately the same size (2827 m^2) and depth (11 m), and were separated by at least 1 km.

Habitat

Macroalgal density was surveyed monthly throughout the study, whereas substrate measurements were only conducted twice as they were not expected to change. At each site, three 30 x 2 m (60 m^2) transects were examined via SCUBA to quantify seasonal variation in the kelp community. The dominant understory kelp in this region includes *Laminaria* spp., *Saccharina* spp., *Agarum clathratum*, *Costaria costata*, and *Cymathaere triplicate* (Chenelot 2003, Hamilton 2004). Six randomly placed 0.25 m^2 quadrats were examined per 60 m^2 transect. All understory kelps in each quadrat were counted. Structurally, understory kelps are very similar with comparable sizes and blade widths, thus they were grouped into two functional understory kelp groups for analysis, small (< 20 cm) and large (>20 cm). Most understory algae were smaller than 15 cm or larger than 25 cm, 20 cm was a natural separation between these groups. The only canopy forming species encountered was *Nereocystis luetkeana,* which, in this region is more sparsely distributed compared to understory species. Because of their relative rarity, all *N. luetkeana* individuals within each 60 m^2 were counted. *Nereocystis luetkeana* individuals greater than 2 m above the substrate were termed large and individuals less than 2 m were termed small.

Rugosity and dominant substrate size were measured in May 2005 and September 2006 along nine 30 m transects at each site via SCUBA. Rugosity is a measure of substrate topography and is a ratio of the topographical distance compared to a straight line distance. Rugosity was measured using a 1 m polyvinyl chloride (PVC) bar with a

length of small mesh (5 mm diameter) chain attached to one end. At six random points along each 30 m transect, the PVC bar was laid perpendicular to the transect, and the chain was placed in the same direction but allowed to drape and follow the substrate topography. At the end of the PVC bar, the chain was marked, straightened, and measured to provide the rugosity ratio. Dominant substrate size was measured by selecting six random points along each 30 m transect and measuring substrate diameter directly beneath that point.

Fish Collections

Fish were collected or observed using a variety of methods during neap tidal cycles from June 2005 to September 2006. Standard Monitoring Units for the Recruitment of Fish (SMURFs) (Findlay & Allen 2002, Steele et al. 2002, Ammann 2004) and light traps (Anderson et al. 2002) were used to catch smaller (< 10 cm) fish, and shrimp pots and diver visual surveys (Bodkin 1986, Hegwer 2003, Hamilton 2004) were used to capture or observe larger fish (> 10 cm). SMURF's and light traps were deployed in mid-water depths, and shrimp pots, diver visual surveys, and SMURF's surveyed the benthos.

SMURFs (Appendix 1) were comprised of 1 x 0.35 m diameter cylinders of fine plastic mesh (2.5 cm), which contained a folded section of larger mesh plastic (5 x 7.5 cm) and were adapted from Ammann (2004). Three SMURFs were deployed per site every month: two in the benthic region (1 m off the substrate) and one in the mid-water (6 m off the substrate). SMURFs were deployed via SCUBA onto moorings and soaked

for 48 hours as intervals greater than 48 hours may decrease recruitment (Ammann 2004). SMURFs were retrieved via SCUBA by enclosing them in a diver propelled collapsing type hoop net to prevent fish escape. The collapsing hoop net or Benthic Ichthyofauna Net for Coral/Kelp Environments (BINCKE) was adapted from Anderson and Carr (1998) with frame measurements of 1.0 x 1.0 m, constructed of PVC and strung with 4.76 mm Ace square mesh netting to form a 1.5 m deep cod end. The BINCKE net and SMURF were brought aboard a research skiff, rinsed vigorously with seawater into a 100 L tote, and run through a 1 cm sieve.

Light traps (Appendix 2, adapted from Anderson et al. 2002 and Calvert 2005) were constructed of a 19 L translucent water container with four funnels facing inward, a PVC pipe with a 330 µm mesh bottom, and two waterproof battery powered Light Emitting Diode (LED) dive flashlights (PrincetonTec. Attitude®) illuminating the trap. As traps were retrieved the contents would drain through a 330 µm sieve, which was then unscrewed and rinsed. Three light traps were deployed in the mid-water (6 m off the substrate) per site every month. Light traps were retrieved via mooring lines after a 48 hour soak time.

Shrimp pots (Appendix 3) were constructed of an 86.0 cm rectangular metal frame covered with 1.25 cm nylon netting with two 10.0 cm entrances. Two shrimp pots baited with herring were randomly deployed in benthic locations at least 5 m apart per site every month. Traps were retrieved after a 48 hour soak time via mooring lines onto a boat in which fish were processed and then released.

SCUBA visual surveys were conducted along three 30 x 2 m (60 m^2) benthic swath transects per site every month during daylight hours. Mooring lines at the center of each site marked a point from which a random distance between 4 and 8 m designated the location where each transect would begin. This was to minimize over-sampling of the mooring region. Visual surveys consisted of two search patterns. In the first, the diver swam out the transect in search of more mobile species within 2 m of the substrate and those that scare off easily. In the second, the diver swam back along the transect returning to the starting point, conducting a more detailed search of the substrate and macroalgae to identify more cryptic species.

All fish captured or observed were identified to the lowest possible taxonomic level using standard references (Eschmeyer et al. 1983, Kessler 1985, Goodson 1988, Matarese et al. 1989, Kramer & O'Connell 1995, O'Clair & O'Clair 1998, Mecklenburg et al. 2002); however, analyses were performed at the family level. Depth of capture was recorded as mid-water, for fish collected 6 m above the substrate, and benthic, for fish collected or observed 1 m above the substrate. Captured fish were measured to the nearest cm whereas fish observed in diver surveys were estimated in 5 cm size classes. As it was impossible to verify sexual maturity and therefore life stage in fish that were not captured, analysis was performed on two fish size classes; smaller fish (< 10 cm) and larger fish (> 10 cm). Fish were separated at 10 cm because there were numerous fish 5 cm or less and 15 cm or greater; 10 cm was a natural division between these groups.

Statistical Analyses

Linear and multivariate statistical techniques were used to examine environmental habitat variables and fish abundance data with STATISTICA v.6 (StatSoft Inc. 2001) and PRIMER v.6 (Clarke & Warwick 2001, Clarke & Gorley 2006). Cluster analysis (Clifford & Stephenson 1975) was used to examine variability among sites based on environmental habitat data. Data were log (x + 1) transformed, ranked, and then resemblance was calculated based on Euclidean distances. One-way analysis of variance (ANOVA) was used to test for spatial variation in substrate measurements. Results were considered significant at $\alpha < 0.05$. Tukey's HSD test was calculated post-hoc on all pairwise comparisons to determine significant differences within groups of three or more. Repeated measures ANOVA was used to test for significant spatial and temporal variation in kelp density across habitat type.

Relative fish abundance (RA) per replicate site was calculated as total fish catch by all gear types combined, then normalized by unit effort with one "effort" defined as one gear deployment of any type or one diver survey. Replicate sites were then combined to get a relative fish abundance in each habitat type. Repeated measures ANOVA was used to test for significant spatial and temporal differences in relative fish abundance among habitat types and by size class. Tukey's HSD test was calculated post-hoc on all pairwise comparisons to determine significant differences in relative abundance among groups of three or more. Results were considered significant at $\alpha < 0.05$. Fish families comprising at least 10% of the total abundance were also analyzed individually by size class for significant spatial and temporal differences in relative abundance among habitat

types. Fish families comprising less than 10% of the total abundance were not analyzed individually, but were included in the analysis among habitat types and in the community analysis.

For each of the dominant families comprising at least 3% of total catch, cluster analysis was used to examine variation in the fish community among habitat types based on relative fish abundance per site. Fish families comprising less than 3% of the total catch were grouped into other fish, and included in community analysis. Fish community data were log (x + 1) transformed and the Bray Curtis dissimilarity coefficient (Bray & Curtis 1957) was calculated.

RESULTS

Habitat

Habitat structural complexity ranged from low (sandy areas with no kelp) to high (understory-canopy kelp regions with large boulders) and varied temporally with changing kelp densities. Cluster analysis grouped the nine sites into three distinct groups based on the similarity of six habitat variables (juvenile understory density, adult understory density, juvenile canopy density, adult canopy density, rugosity, and dominant substrate size) (Fig. 2). The six kelp sites grouped separately from the sand sites (Fig. 2). The three canopy sites grouped separately from the understory sites indicating kelp community differences, likely due to the presence of *Nereocystis luetkeana* (Fig. 2).

The substrate complexity measurements of rugosity and dominant substrate size were significantly different among habitats (Table 1). Sandy sites had significantly lower

rugosities than understory ($H = 20.76$, $p < 0.001$, $n = 306$) and canopy ($H = 18.36$, $p < 0.001$ $n = 306$) kelp sites. Understory sites had slightly higher mean rugosity values than canopy sites (Table 2), but this difference was not significant ($H = 2.43$, $p = 0.198$, $n = 306$, Table 2). Dominant substrate size of sand habitats was significantly smaller than those of understory ($H = 36.06$, $p < 0.001$, $n = 396$) and canopy kelp sites ($H = 40.23$, $p < 0.001$ $n = 396$). Canopy sites had slightly higher mean substrate size than understory sites (Table 2), but this difference was not significant ($H = 2.42$, $p = 0.202$, $n = 396$).

Understory and canopy kelp communities showed spatial and temporal variation. Understory kelp density varied significantly over time and among habitat types (Table 1). Understory kelp densities were highest during summer months and lowest during winter. Significant differences were evident in understory density among the three habitats (Table 1). Sand sites had the lowest mean understory kelp density with canopy sites having the highest (Table 2). The variation in canopy kelp density was also significant over time and by habitat (Table 1). Canopy kelp densities were highest during summer months and lowest during winter. Canopy sites contained significantly more *Nereocystis luetkeana* ($H = 12.83$, $p < 0.001$, $n = 432$) than understory sites. *Nereocystis luetkeana* was not encountered at sand sites.

Fish

A total of 2732 fish from fifteen families were either captured or observed (Table 3). Of these, four families dominated in total abundance contributing at least 10% of the

total catch: Gadidae 29.1%, Pleuronectidae 18.9%, Hexagrammidae 16.9%, and Sebastidae 16.2%. These four families cumulatively contributed 81.1% to the total catch.

Total Fish Abundance

Overall, relative fish abundance showed significant variation over time, by depth of capture, by family of fish, and among habitats, but was not significant when comparing relative abundance of smaller versus larger fish (Table 4). Relative fish abundance varied significantly over time (Figs. 3 & 4), with increased abundance in summer and decreased abundance in winter. Relative fish abundance in benthic samples (RA = 0.137 ± 0.009 s.e.) was significantly higher ($H = 9.74$, $p < 0.001$, $n = 8336$) than that in mid-water samples (RA = 0.036 ± 0.013 s.e.). The relative abundance of smaller mid-water and benthic fish were similar ($H = 2.89$, $p = 0.171$, $n = 4168$), thus the difference in abundance by depth of capture was caused by higher abundance of larger fish in benthic samples. Because no large fish were encountered in the mid-water and smaller fish showed no significant variation when comparing mid-water versus benthic samples, benthic and mid-water samples were pooled, thus removing depth of capture as a covariate.

Significant differences were identified in relative fish abundance when examining fish families (Tables 3 & 4). Gadid abundance was significantly higher than hexagrammid ($H = 5.08$, $p = 0.008$, $n = 2084$) and sebastid, ($H = 5.11$, $p = 0.007$, $n = 2084$), but similar to pleuronectid abundance ($H = 3.97$, $p = 0.094$, $n = 2084$). Pleuronectids, hexagrammids, and sebastids all had similar abundances (Table 2).

Relative fish abundance was significantly different among habitat types (Table 4) with highest abundances in understory kelp sites and the least in canopy kelp sites (Table 2). Overall smaller fish were slightly more abundant than larger fish (Table 2), but this difference was not statistically significant (Table 4). However, there were significant interactions between habitat and life stage (Table 4). Smaller fish were more abundant than large fish in sand habitats (Table 2; $H = 4.93$, $p = 0.006$, $n = 8336$), mainly because of high abundances of small pleuronectids (Fig 3). Larger fish were significantly more abundant in understory habitats than small fish (Table 2; $H = 5.47$, $p = 0.002$, $n= 8336$), mainly because of high abundances of large sebastids (Fig. 3). Canopy sites had similar abundances of small and large fish (Table 2).

Fish Family Analysis

When examining each of the dominant four families encountered independently, they all showed significant variation in relative abundance temporally, spatially, and in relation to size class. Each family however, had a unique distribution over time, by habitat type, and depending on the size of fish.

Gadids, mainly Pacific cod (*Gadus macrocephalus*, Appendix 4), showed significant differences in relative fish abundance temporally, by size class, and across habitats (Table 5). The occurrence of smaller gadids fluctuated temporally with highest abundances in summer and no fish in winter, whereas larger gadid abundance remained temporally consistent (Figs. 3a & 4a). The total abundance of smaller gadids was significantly greater than that of larger fish (Table 5, Figs. 3a & 4a). Small gadids utilized

understory ($H = 8.85$, $p < 0.001$, $n = 1042$) and canopy sites ($H = 13.15$, $p < 0.001$ $n = 1042$) significantly more than sandy sites, with slightly higher relative abundance in canopy than understory sites (Table 2). Larger gadids were evenly distributed across all habitats (Fig. 4a).

The pleuronectids also showed significant differences in relative fish abundance temporally, by size class, and across habitats (Table 5). The most common pleuronectid was rock sole (*Lepidopsetta spp.*, Appendix 4). The abundance of small and large fish fluctuated throughout the year, with increased abundances in summer decreasing to zero during winter (Figs. 3b & 4b). The total abundance of small pleuronectids was significantly greater than that of large fish (Table 5, Figs. 3b & 4b). Small fish utilized sandy habitats exclusively showing significantly higher abundance there than in understory ($H = 18.84$, $p < 0.001$, $n = 1042$) or canopy habitats ($H = 18.84$, $p < 0.001$, $n = 1042$, Fig. 3b). Large fish, although only found in sandy habitats (Fig. 4b), did not show significant differences among habitat types due to a large variance in relative abundance.

Hexagrammid abundance varied significantly temporally, by size class, and across habitats (Table 5). There were three dominant hexagrammid species (appendix 4): kelp greenling (*Hexagrammos decagrammus*), whitespotted greenling (*H. stelleri*), and rock greenling (*H. lagocephalus*). Larger fish were most abundant in summer and least abundant in winter (Fig. 4c). Small fish were only captured during summer months (Fig. 5c). The total abundance of large hexagrammids was significantly greater than that of small hexagrammids (Table 5, Figs. 3c & 4c). Large hexagrammids had significantly higher abundance in understory ($H = 9.53$, $p < 0.001$, $n = 1042$) and canopy sites ($H =$

7.25, $p < 0.001$, $n = 1042$) than in sand sites, with slightly higher averages in understory sites (Table 2). Smaller fish were almost absent from the study, and only encountered in sand and canopy habitats (Fig. 3c).

The sebastids showed significant differences in relative fish abundance temporally, in relation to size class, and across habitats (Table 5). Sebastids consisted of mainly black rockfish (*Sebastes melanops*) and dusky rockfish (*S. ciliatus*) (Appendix 4). Both small and large fish had higher abundances during summer, which decreased to zero during winter (Figs. 3d & 4d). Large fish had a significantly higher total abundance than small fish (Table 5, Figs. 3d & 4d), and occurred almost exclusively in understory habitats, having significantly higher abundances, than both sand ($H = 15.34$, $p < 0.001$, $n = 1042$) and canopy sites ($H = 15.22$, $p < 0.001$, $n = 1042$, Fig. 4d). Smaller fish were ubiquitous across habitat types (Fig. 3d).

Fish Community

Fish community cluster dendrograms revealed distinct relationships between fish community composition and habitat type (Fig. 5). Understory kelp sites had the most similar fish communities, with at least 83% similarity among these sites (Fig. 5a). All canopy kelp sites had fish communities that were at least 81% similar while sand sites had the lowest similarity among sites, at least 68%. Overall, kelp sites were more similar to one another than to sandy sites, being 73% similar. A cluster dendrogram for the smaller fish community revealed two distinct groups (Fig. 5b). All kelp sites, including canopy and understory, had at least 76% similar communities, while sand sites clustered

with at least 67% similarity. The smaller fish community was 53% similar among all sites and habitats. The three different habitat types all grouped out separately based on the large fish community (Fig. 5c). Canopy sites were most similar at 85% followed closely by understory 84% and lastly sand 65% (Fig. 5c). The large fish community was 41% similar among all sites and habitats (Fig. 5c).

DISCUSSION

Although habitat complexity can be strongly correlated to fish abundance and diversity in many cases (Bell & Galzin 1984, Roberts & Ormond 1987, Willis & Anderson 2003), examinations of macroalgal density effects on fish populations are sparse (Carr 1994, Willis & Anderson 2003, Hamilton 2004), especially in higher latitudes. Furthermore, many studies fail to examine the effects of habitat complexity on different fish families (Hixon & Beets 1993, Almany 2004a), neglecting the fact that fish utilize habitats in unique ways depending on fish family and/or species. This study used multiple gear types to attempt to describe the effects of increasingly complex rocky kelp habitats on fish communities in these high latitude temperate waters. The dominant families encountered were all either commercially or recreationally important and the rocky kelp habitats examined here are likely crucial to many of their life histories.

Habitat structural complexity does not appear to be a determinant of total fish abundance in macroalgal environments within Kachemak Bay, Alaska. It was expected that fish abundances would be greatest in the canopy habitats as they are most complex. However, total fish abundance was greatest in the medium complexity understory habitat.

When examining habitat use of different size classes of fish, medium and low complexity sites still supported higher abundances of fishes with small fish abundance being highest at sand sites and large fish abundance greatest at understory sites. These data do not support the first hypothesis that increasingly complex habitats have higher abundances of both juvenile and adult fish. Others have documented similar patterns where total fish abundance in complex environments was not solely related to kelp density (Angel & Ojeda 2001, Willis & Anderson 2003). This phenomenon is likely the result of fish families or species utilizing habitats for different reasons. It is apparent that not all fish species will select the most complex habitat and some may select low complexity habitats. Pleuronectids exemplify this observation by preferring sand habitats (Norcross et al. 1995, Norcross et al. 1999, Abookire et al. 2001) and may be partially responsible for these results. This makes broad characterizations about total fish abundance and distribution difficult and demonstrates the need for a species-specific approach when examining or classifying fish habitat.

The results of this study support the second hypothesis that habitat complexity has different effects on fish distribution depending on family. Previous studies have found varying effects of habitat complexity on fish assemblages by species and size (Willis & Anderson 2003, Almany 2004a), but they all indicate that predation was the most influential factor responsible for fish community composition. While the present study did not examine predation, it is possible that predation influenced the fish communities in Kachemak Bay, Alaska. Some species' abundances, such as greenlings and rockfish, were higher in complex habitats. These species may be more adapted to utilize complex

structure and may have lower mortality rates there. Predation may also be influencing the fish community in the lower complexity habitats as well, resulting in more cryptic species, such as flatfishes, that can bury themselves in the sand to lower their predation rates.

The fish community within each of the three habitats was more similar than across habitat types, supporting the third hypothesis. Each of these habitats is characterized by a few dominant fish species, all likely utilizing the given habitat for a particular attribute. These habitat preferences may not be identical for different sized fish of one species, thus requiring examination of community structure using different fish size classes. The smaller fish community in this study was similar across both kelp habitats, indicating that the added complexity from the canopy kelp was not critical to smaller fish. These smaller fish may be utilizing the understory kelp much like many juvenile fish utilize seagrass habitats in other regions (Ogden 1988, Baelde 1990, Laurel et al. 2003). Functionally, understory kelp is very similar to seagrass in that it reduces water flow and creates refuge (Eckman et al. 1989). Because understory kelp can be much denser than seagrass in these regions (Markis personal observation) it may support greater fish abundances.

The results presented here suggest that the differences in the larger fish community among habitat types may be from something other than increased canopy kelp densities. In contrast to this study, in which none of the dominant fish families had increased abundances in canopy sites, many previous studies document fish associations with canopy-forming kelp (Carr 1994, Dean et al. 2000, Anderson 1994). In other areas

where canopy-forming kelp benefited fish populations, the kelp was mainly *Macrocystis pyrifera,* which provides more mid-water structure than the *Nereocystis luetkeana* examined in this study. It is possible that the added complexity afforded by the *N. luetkeana* is not sufficient to increase fish abundances. Alternatively, because the majority of fish species examined were demersal, they may not be able to utilize the added complexity from *N. luetkeana* higher in the water column, and thus, were influenced primarily by substrate characteristics and understory kelp species.

Closer examination of the four dominant fish families encountered in this study allows for a more detailed assessment of habitat preferences. The gadids encountered in this study appeared to be Pacific cod, which are schooling fish typically associated with demersal habitats. Smaller gadids were likely young-of-the-year and larger fish were likely juveniles of ages 1, 2, or 3 (Gustafson et al. 2000, Abookire et al. 2001). Gadids were usually sighted within 2 m of the substrate, but were rarely sighted within the understory kelp layer. As a diver approached, gadids would typically move closer to the understory kelp and then use the kelp for cover (Markis, personal observation). The association between smaller young-of-the-year gadids and understory kelp and these observations suggests the potential for these habitats to be used as nurseries, feeding grounds, and refuge. These results are contradictory to a previous study that found no association between Pacific cod distribution and macroalgal or eelgrass presence around Kodiak Island (Abookire et al. 2007), which is < 200 km from Kachemak Bay. Discrepancies between the present study and Abookire et al. (2007) may be due to gear biases. The beach seine and small mesh beam trawl used by Abookire et al. (2007) are

inadequate for sampling rocky kelp environments. It is possible that a negative correlation exists between macroalgae and juvenile Pacific cod, but only at macroalgal densities low enough to seine and trawl. Macroalgal densities examined in the present study would not have permitted seining or trawling. Studies in nearby Prince William Sound, Alaska found similar results to the present study where positive correlations between Pacific cod and macrophyte distribution where identified (Laur and Haldorson 1996, Dean et al. 2000). The larger Pacific cod shifted their habitat use from kelp habitats to sandy areas as they grew, potentially no longer needing the kelp for refuge.

The temporal variation in abundance of small Pacific cod in this study was similar to that of others (Abookire et al. 2001, Abookire et al. 2007) in which juvenile fish were captured from April to August, but not during winter months. It is likely that in winter, Pacific cod move offshore into the deeper waters of the shelf break region (Hart 1973, Gustafson et al. 2000). The timing of small Pacific cod habitat associations could be linked to macroalgal presence. With most understory species being annuals, the small Pacific cod possibly migrate offshore when the kelps start dying and there is little refuge available in nearshore areas. It is also possible that the timing of Pacific cod habitat associations is linked to some abiotic environmental variable that was not measured, such as temperature and salinity. Other work in this area suggests that salinity may be important, but failed to find associations between temperature and Pacific cod distribution (Abookire et al. 2007).

Pleuronectids encountered in this study appeared to be rock sole and were captured almost exclusively in sandy habitats. This is similar to habitat association

patterns described in several previous studies (Norcross et al. 1995, Norcross et al. 1999, Abookire et al. 2001). The temporal variation in abundance of pleuronectids was similar to patterns found by others (Abookire et al. 2001, Abookire et al. 2007), with individuals encountered from April to November, but absent during winter. The present study substantiates previously reported habitat associations and specifically failed to find any association between pleuronectid distribution and rocky macroalgal habitats at any time over the year. These results agree with earlier findings (Moles & Norcross 1995, Norcross et al. 1995, Norcross et al. 1999, Abookire et al. 2001) and demonstrate the importance of shallow nearshore sand habitats to juvenile pleuronectids in this region.

Juvenile hexagrammid distribution is not well understood, but it is likely that they were residing in habitats other than the nearshore subtidal environment examined in this study. In the Sea of Japan, a juvenile hexagrammid, the masked greenling (*Hexagrammos octogrammus*), was found to inhabit the rocky littoral zone (Gomelyuk & Leunov 1999). If the hexagrammids encountered in the present study have juvenile stages that inhabit rocky littoral zones they would have been missed because sampling focused on subtidal habitats.

Adult hexagrammids are demersal nest brooders laying and guarding eggs in rocky kelp habitats (Low & Beamish 1978, Crow et al. 1997). For this reason, the distribution of large hexagrammids in kelp habitats seen in the present study is not surprising. It is likely that these rocky kelp habitats are essential for many adult hexagrammids and this work affirms habitat associations documented by others (Eschmeyer et al. 1983, Dean et al. 2000, Hamilton 2004).

Because sebastids are typically associated with rocky kelp habitats (Carr 1991, Ammann 2004), it would be expected that highly complex habitats would support greater sebastid abundances. Unexpectedly, smaller sebastids were encountered in all habitats, including sandy locations. This distribution pattern may be a sampling artifact caused by SMURF's. The majority of the smaller sebastids came from SMURF captures. Capture by SMURF relies on fish entering the trap. Fish are less likely to inhabit artificial SMURF's in areas with ample natural refuge. However, in sandy areas with no refuge, fish are more likely to inhabit artificial traps, accounting for higher than expected capture rates in sandy sites. Similar responses with increased abundances of fish being encountered in sandy habitats when refuge is added have been observed when transplanting coral into sandy environments (Nanami & Nishihira 2003). With the likelihood that SMURF's may have higher capture rates in areas lacking natural refuge, it is believed that smaller sebastid distribution is a result of gear bias and that natural distribution would more closely follow that of larger fish.

The larger sebastid distribution identified in this study may indicate that these fishes are utilizing habitats for attributes that were not investigated. The fact that sebastids were almost exclusively captured in understory habitats is contradictory to what others have found with adult rockfish being strongly associated with canopy forming kelp species (Bodkin 1986). Either the added complexity provided by the canopy kelp *Nereocystis luetkeana* had a negative affect on sebastid abundance in the present study, or there is some other parameter that was not detected through the substrate measurements examined. It is not expected that *N. luetkeana* had a negative effect on sebastid

abundance. Others have described substrate crevice characteristics (such as size, depth, diameter, and number of holes) as factors that contribute to fish abundance (Friedlander & Parish 1998, Almany 2004a). Although the present study measured rugosity and dominant substrate size, it is possible that understory and canopy sites had differing crevice characteristics and these attributes are responsible for the differences in larger sebastid abundances.

The different effects of habitat complexity on fish abundance and community composition point out the need for examining fish habitat on a more detailed level in order to determine complicated interactions between marine fish and their habitat. The results of this study indicate that specific groups or even fish species are utilizing different habitats, but this study was only able to examine habitat associations. Future efforts should be focused on the more difficult question of determining causalities of nearshore fish distribution. It is recommended that fish habitat be examined on a species by species basis and that particular attention be paid to substrate characteristics.

In conclusion, this was a broad examination of habitat use by fishes in different nearshore habitats. Several conclusions from this study may be applicable to other regions or future research. First, fish families are associated with different habitats spatially, temporally, and by size class. Therefore, broad conclusions about fish abundance in any particular time, habitat, or life stage are tenuous at best. This study points out that overall fish abundance was significantly different in habitats of varying structural complexity, but closer examination showed that different fish families respond in varying ways to added habitat complexity. Second, using multiple gear types as in this

study may yield different results than studies using only one or two gear types when collecting fish in complex nearshore habitats. This is especially true for smaller fish. The present study used multiple gear types in an effort to try and characterize the fish community as accurately as possible. Future studies should take into consideration the differing effects of varying habitat complexity levels as they may be influencing the fish community and would benefit from more detailed causative approaches examining habitat associations for individual fish species.

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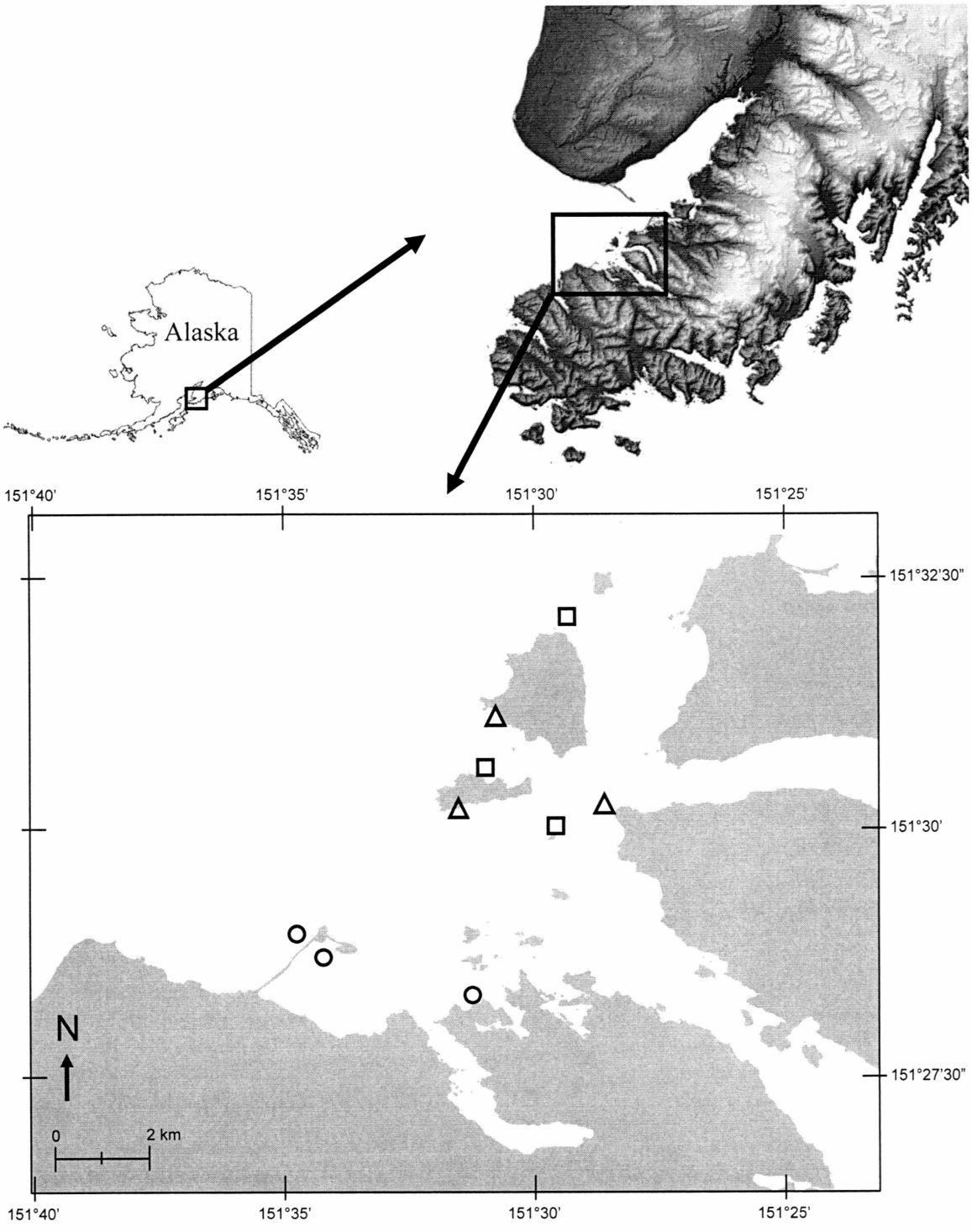


Figure 1. Map of study sites within Kachemak Bay, Alaska. Location of replicate sand (circles), understory (triangle), and canopy (square) sites.

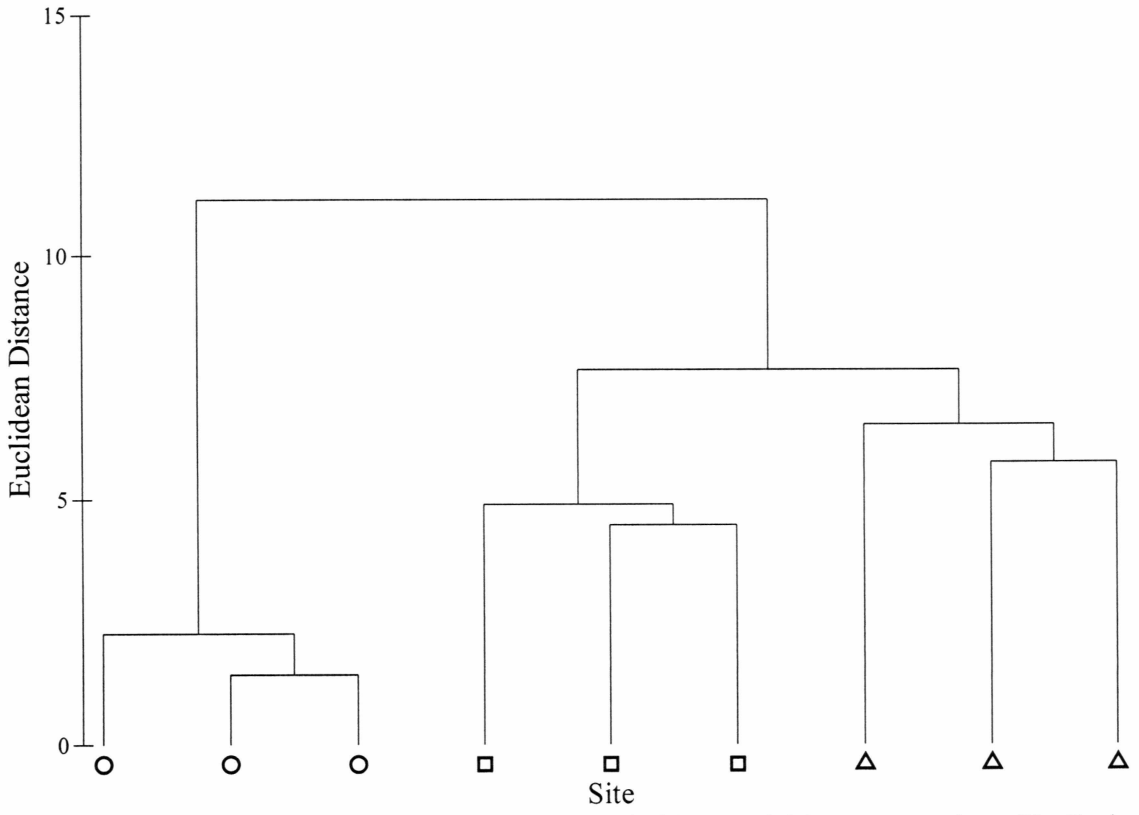


Figure 2. Cluster analysis depicting similarity in habitat variables among sites. Similarity in replicate sand (circles), understory (triangle), and canopy (square) sites based on six environmental habitat measurements. Average rugosity, dominant substrate size, and kelp density was calculated for each site. Average kelp density was calculated for small understory, large understory, small canopy, and large canopy kelps.

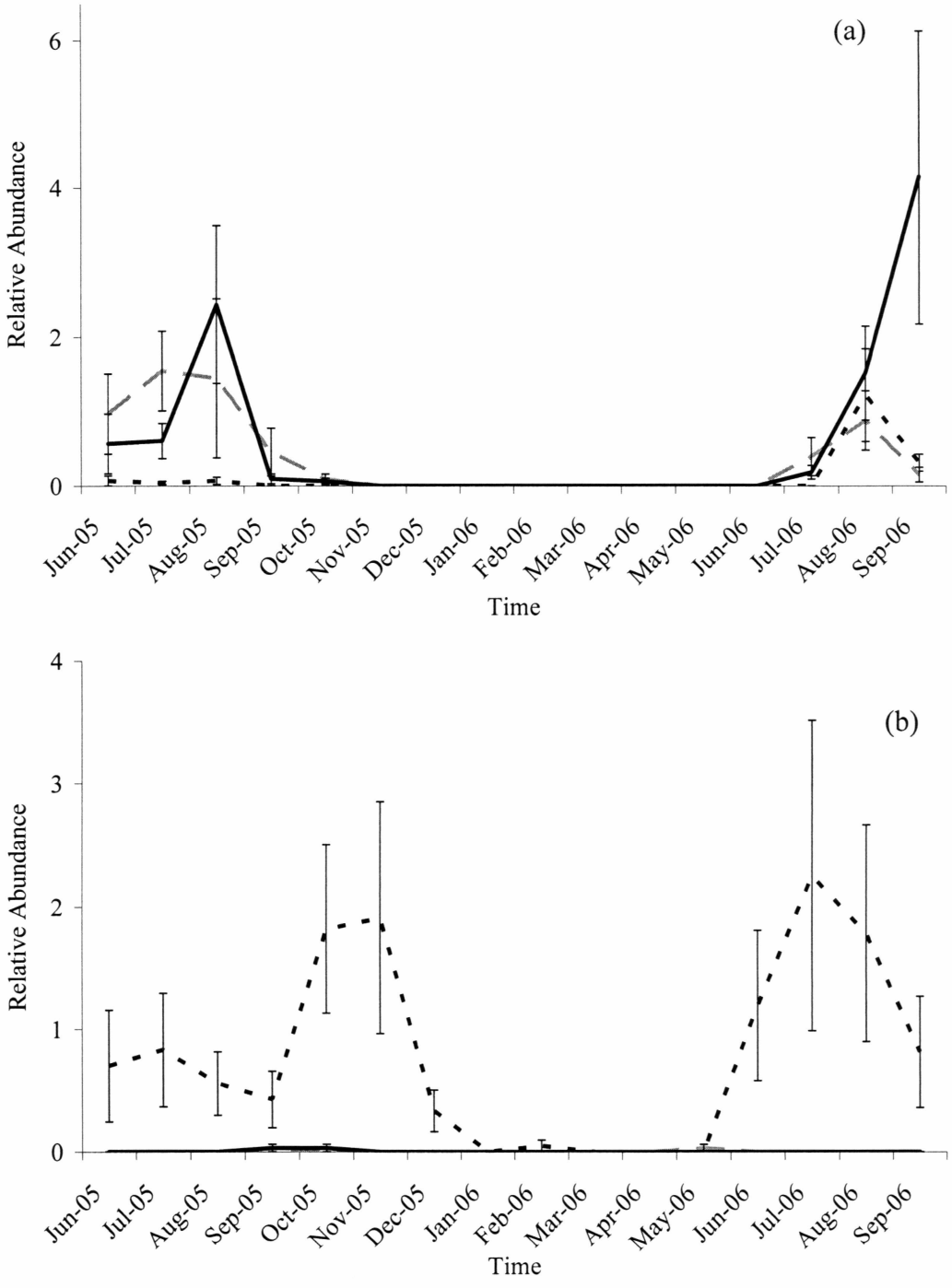
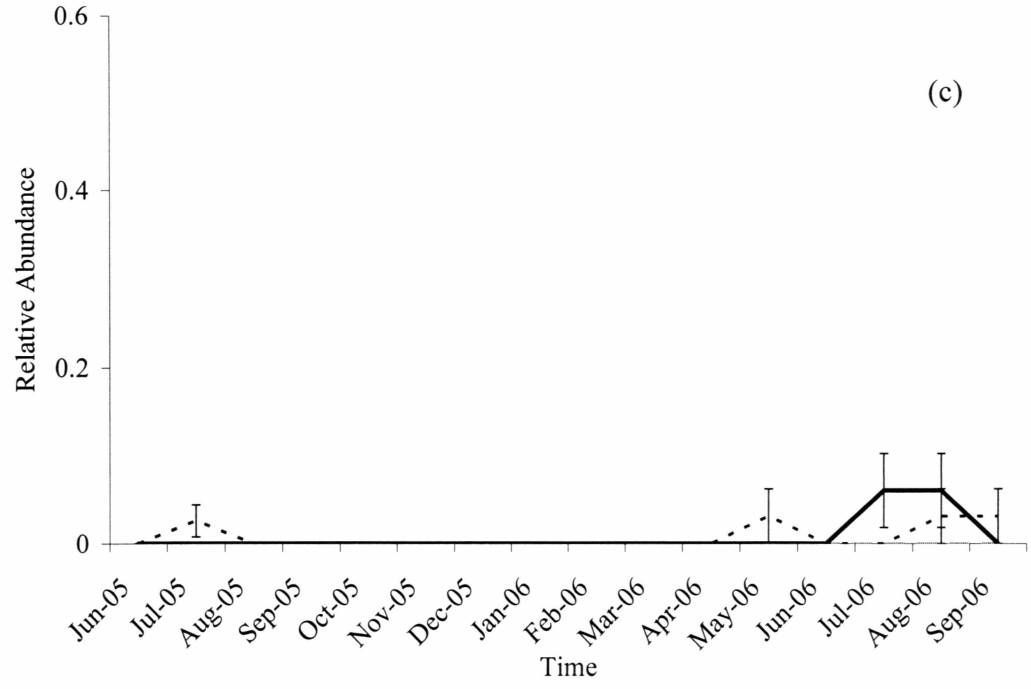


Figure 3. Mean relative abundance of small fishes over time. Relative abundance (± 1 SE) of < 10 cm (a) Gadidae, (b) Pleuronectidae, (c) Hexagrammidae, and (d) Sebastidae fishes captured or encountered in sand (dotted), understory (dashed), and canopy (solid) habitats over time. Only families comprising more than 10% of total catch are depicted.



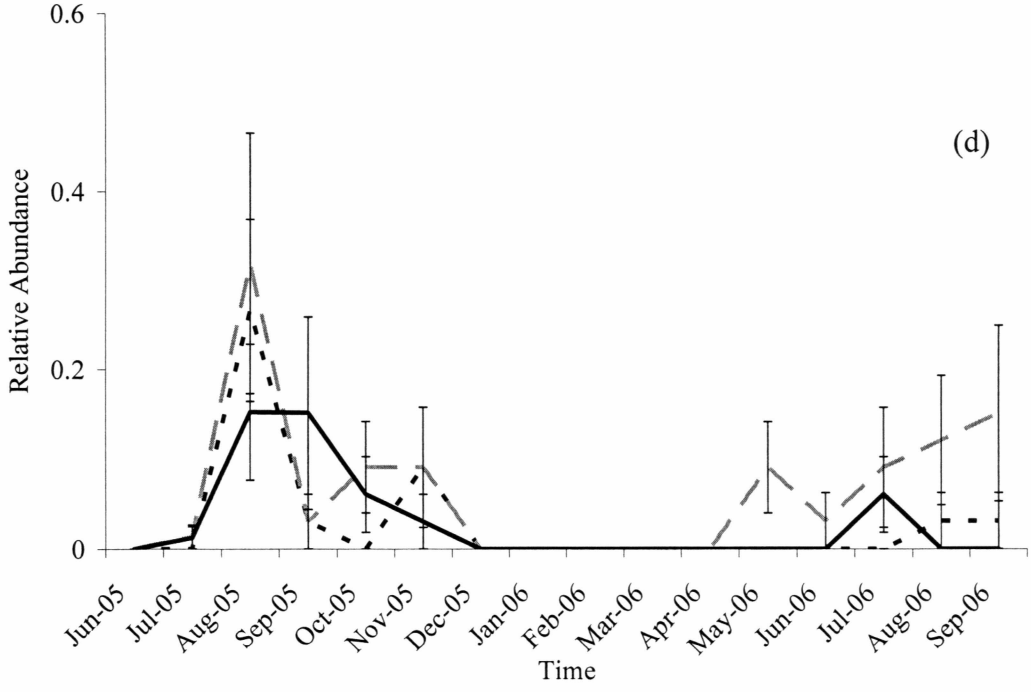


Figure 3 continued. Mean relative abundance of small fishes over time. Relative abundance (± 1 SE) of < 10 cm (a) Gadidae, (b) Pleuronectidae, (c) Hexagrammidae, and (d) Sebastidae fishes captured or encountered in sand (dotted), understory (dashed), and canopy (solid) habitats over time. Only families comprising more than 10% of total catch are depicted.

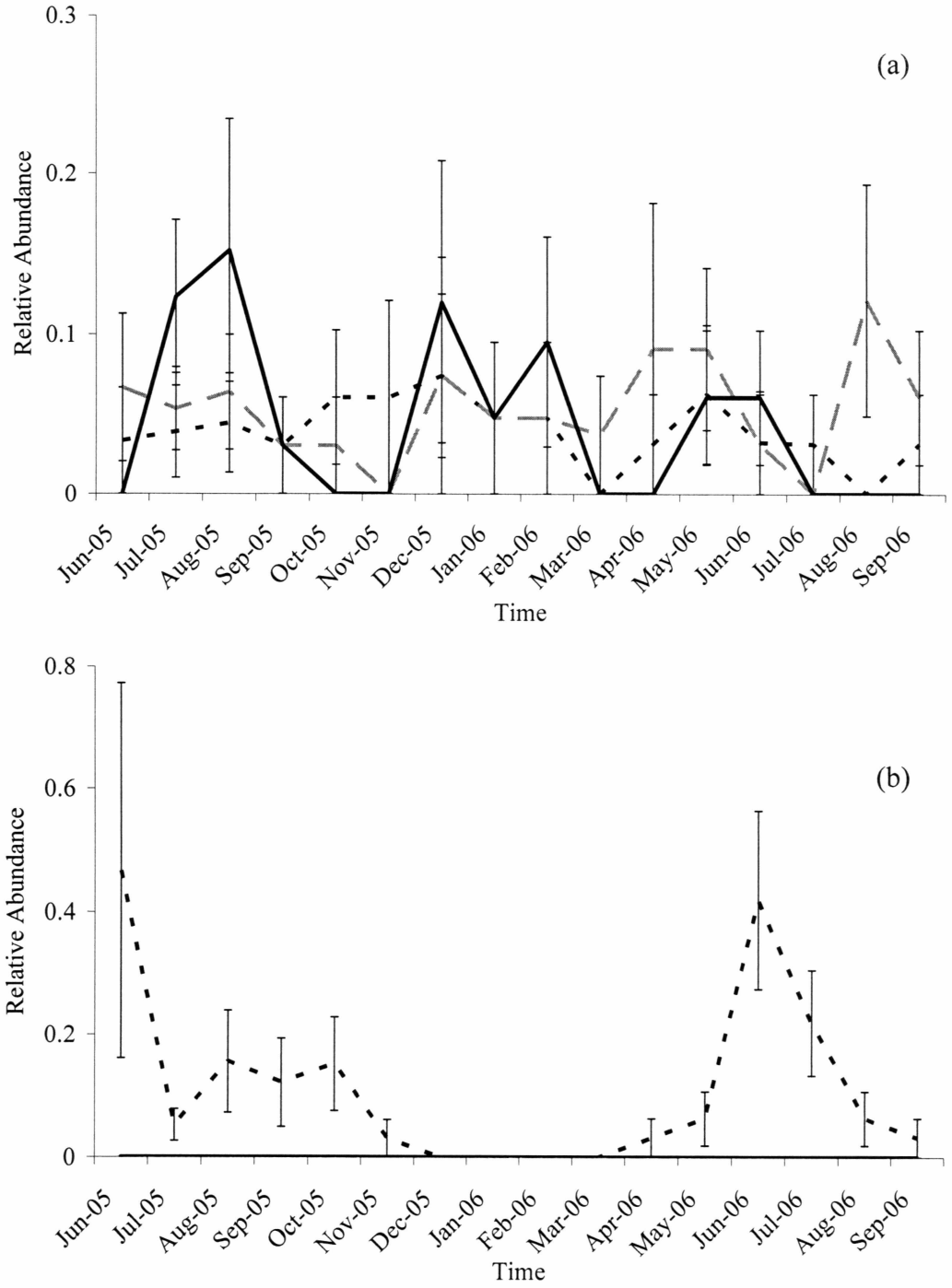


Figure 4. Mean relative abundance of large fishes over time. Relative abundance (± 1 SE) of > 10 cm (a) Gadidae, (b) Pleuronectidae, (c) Hexagrammidae, and (d) Sebastidae fishes captured or encountered in sand (dotted), understory (dashed), or canopy (solid) habitats over time. Only families comprising more than 10% of total catch are depicted.

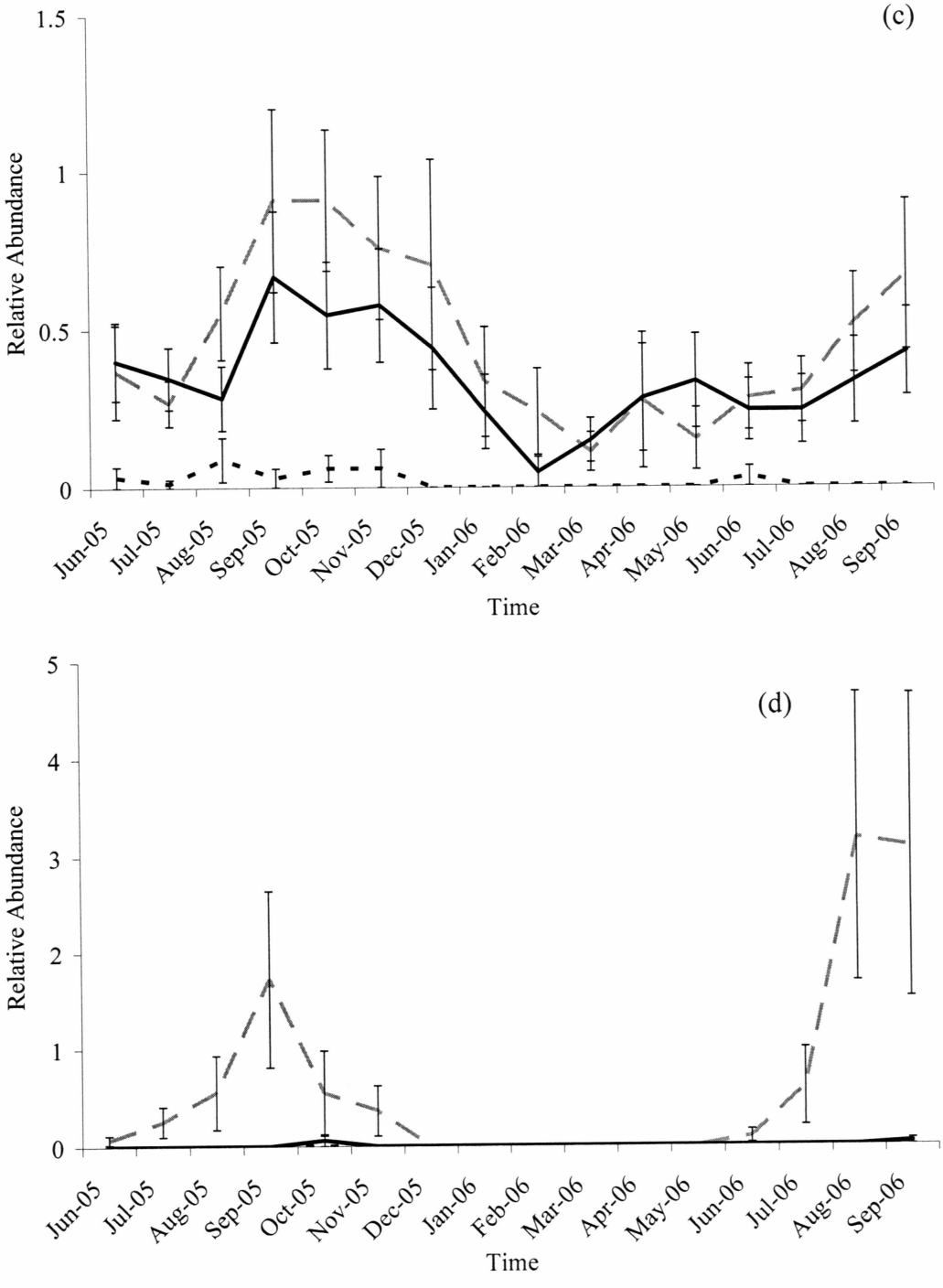


Figure 4 continued. Mean relative abundance of large fishes over time. Relative abundance (± 1 SE) of > 10 cm (a) Gadidae, (b) Pleuronectidae, (c) Hexagrammidae, and (d) Sebastidae fishes captured or encountered in sand (dotted), understory (dashed), or canopy (solid) habitats over time. Only families comprising more than 10% of total catch are depicted.

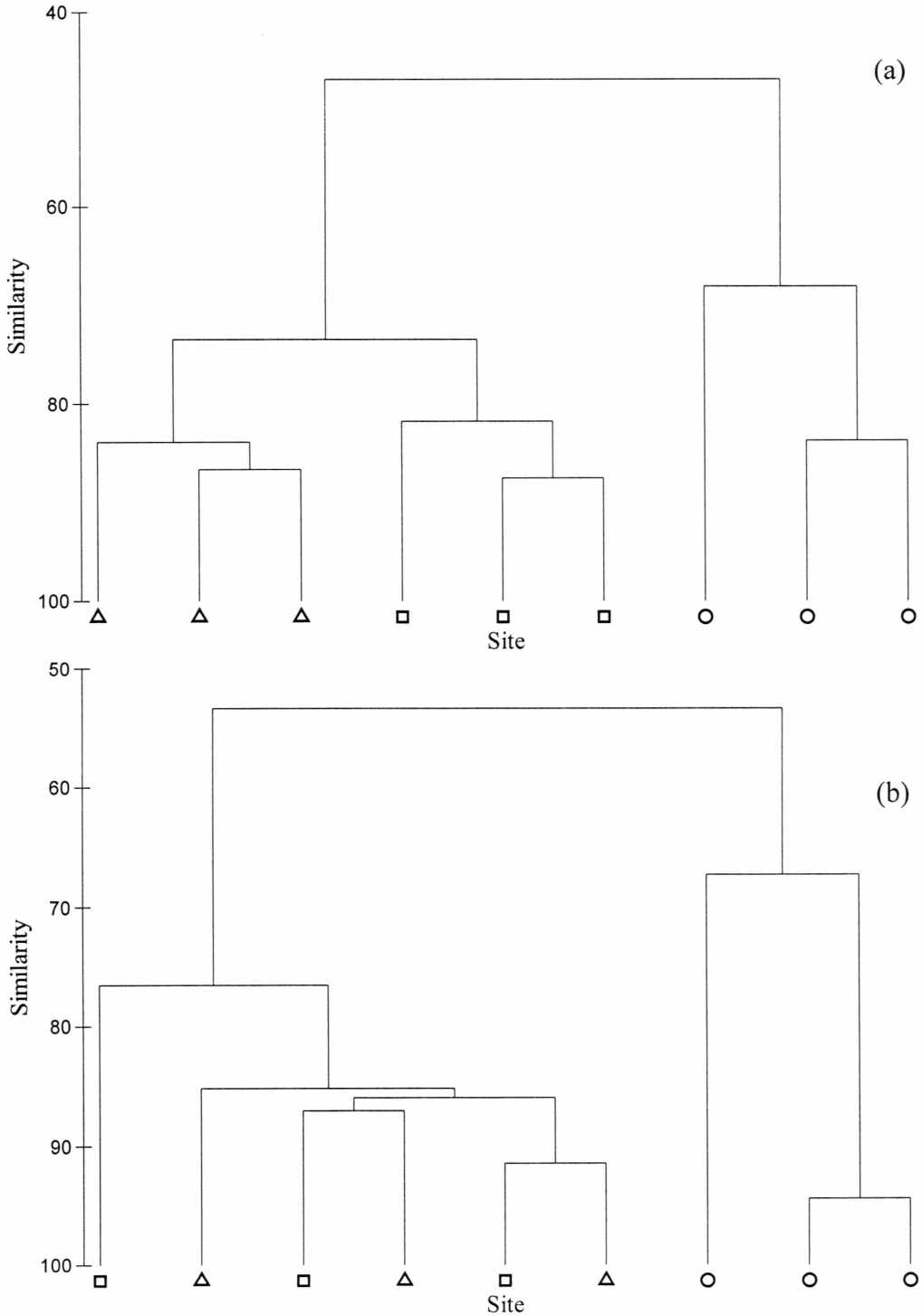


Figure 5. Cluster analysis depicting similarity in the fish community among sites. Similarity in replicate sand (circles), understory (triangles), and canopy (squares) sites for (a) total, (b) smaller, and (c) larger fish abundance based on average relative abundance per site in each of the dominant families (comprising at least 3% of total abundance).

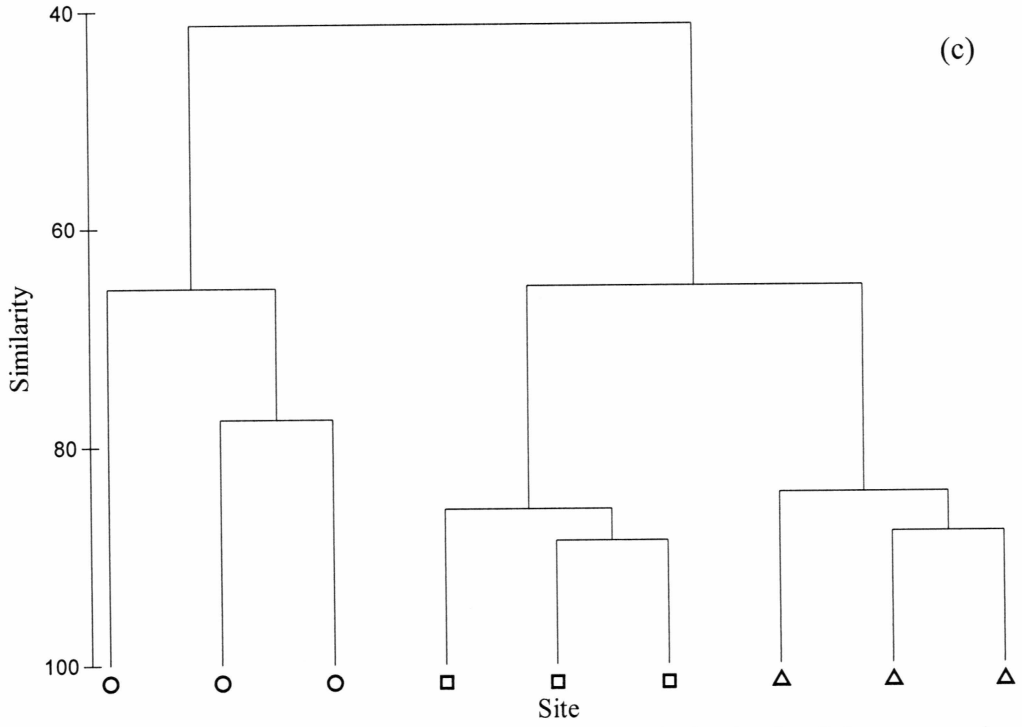


Figure 5 continued. Cluster analysis depicting similarity in the fish community among sites. Similarity in replicate sand (circles), understory (triangles), and canopy (squares) sites for (a) total, (b) smaller, and (c) larger fish abundance based on average relative abundance per site in each of the dominant families (comprising at least 3% of total abundance).

Table 1. ANOVA statistics for habitat variables. One-way and repeated measure ANOVA for habitat complexity measurements. Habitat represents differences in sand, understory, and canopy habitats.

Rugosity	SS	DF	MS	F	P
Habitat	11.25	2	5.62	129.04	<0.001
Error	19.83	455	0.04		
Dom. Sub. Size					
Habitat	51088.79	2	25544.39	496.32	<0.001
Error	28822.13	560	51.47		
Understory Kelp					
Time	1593.07	15	106.20	11.97	<0.001
Error	7365.27	830	8.87		
Habitat	8266.49	2	4133.25	398.15	<0.001
Habitat x Time	1499.22	30	49.97	4.81	<0.001
Error	17232.65	1660	10.38		
Canopy Kelp					
Time	1224.31	15	81.62	3.70	<0.001
Error	2820.00	128	22.03		
Habitat	2542.72	2	1271.36	55.91	<0.001
Habitat x Time	2392.39	30	79.75	3.51	<0.001
Error	5820.89	256	22.74		

Table 2. Mean values for habitat complexity and fish abundance by habitat. Habitat and fish measurements averaged over sand, understory, and canopy sites (± 1 s.e.).

	Sand	Understory	Canopy
Habitat			
Rugosity	1.00 ± 0.00	1.35 ± 0.02	1.31 ± 0.02
Dom Substrate Size (cm)	0.01 ± 0.00	19.23 ± 0.56	20.52 ± 0.51
Understory Kelp Density (stipes/0.25m^2)	0.08 ± 0.02	3.02 ± 0.12	4.41 ± 0.14
Canopy Kelp Density (stipes/30m^2)	0.00 ± 0.00	0.10 ± 0.05	5.20 ± 0.68
Total Fish			
Total Fish Abundance (RA)	0.09 ± 0.01	0.14 ± 0.01	0.08 ± 0.01
Small Fish Abundance (RA)	0.14 ± 0.02	0.09 ± 0.02	0.11 ± 0.02
Large Fish Abundance (RA)	0.05 ± 0.01	0.18 ± 0.02	0.06 ± 0.01
Fish by Family			
Small Gadidae (RA)	0.11 ± 0.04	0.51 ± 0.13	0.69 ± 0.16
Large Gadidae (RA)	0.04 ± 0.01	0.05 ± 0.01	0.05 ± 0.01
Small Pleuronectidae (RA)	0.83 ± 0.15	0.00 ± 0.00	0.00 ± 0.00
Large Pleuronectidae (RA)	0.11 ± 0.02	0.00 ± -	0.00 ± -
Small Hexagrammidae (RA)	0.01 ± 0.00	0.00 ± -	0.01 ± 0.00
Large Hexagrammidae (RA)	0.02 ± 0.01	0.46 ± 0.04	0.35 ± 0.03
Small Sebastidae (RA)	0.03 ± 0.01	0.07 ± 0.02	0.03 ± 0.01
Large Sebastidae (RA)	0.00 ± -	0.67 ± 0.16	0.01 ± 0.00

Table 3. Total number of small and large fish captured by gear type. Fish < 10 cm and > 10 cm captured or observed in benthic and mid-water samples. Families comprising less than 3% of the total catch were grouped into Other (- indicates no fish).

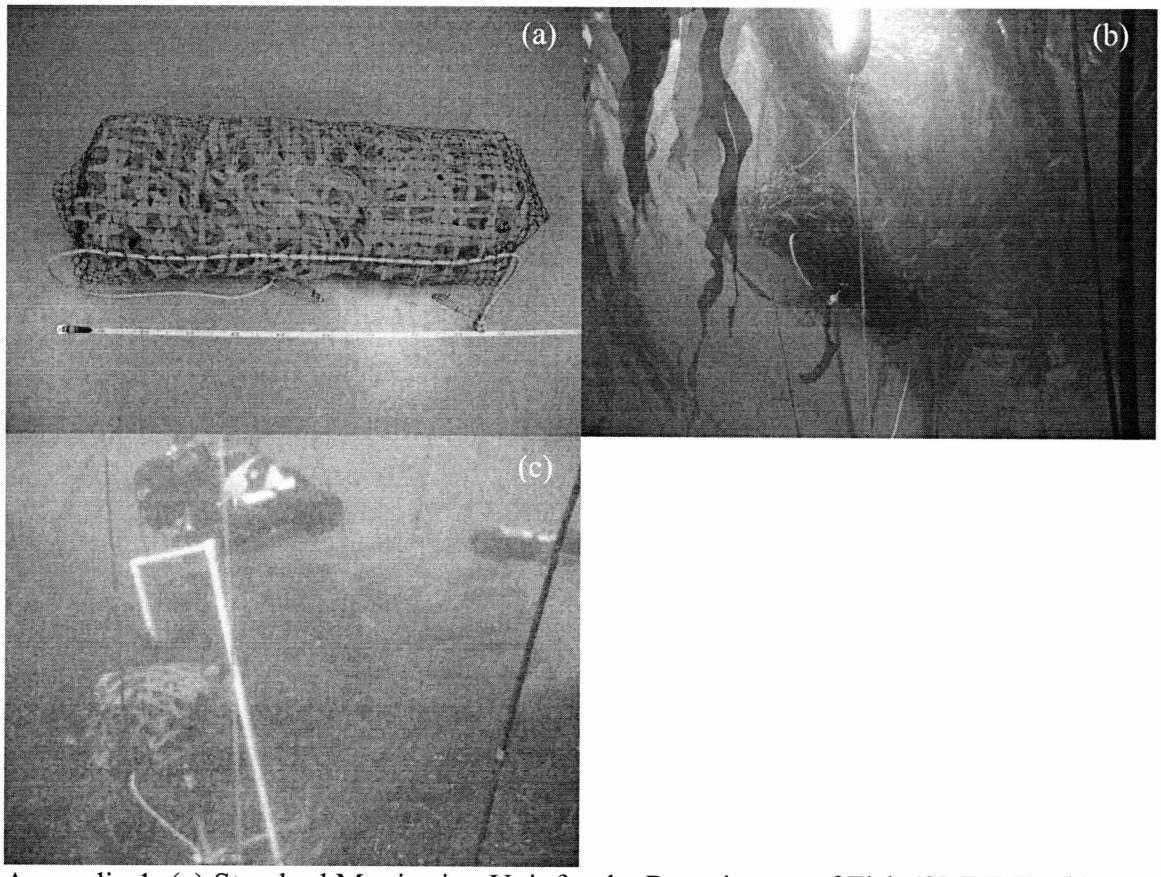
	Benthic Samples						Midwater Samples				Total Small	Total Large	Total
	Diver Visual		Shrimp Pot		SMURF		SMURF		Light Trap				
	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large			
Gadidae	497	10	7	67	-	-	-	-	215	-	719	77	796
Pleuronectidae	351	34	-	29	-	-	-	-	103	-	454	63	517
Hexagrammidae	6	257	1	192	-	-	2	-	3	-	12	449	461
Sebastidae	32	368	-	-	27	-	15	-	1	-	75	368	443
Cottidae	47	40	-	86	55	-	16	-	5	-	123	126	249
Bathymasteridae	-	83	-	13	-	-	-	-	-	-	0	96	96
Clupeidae	-	54	-	-	-	-	-	-	7	-	7	54	61
Stichaeidae	1	10	-	1	1	-	2	-	10	-	14	11	25
Ammodytidae	-	11	-	-	-	-	-	-	7	-	7	11	18
Liparidae	-	-	-	-	5	-	6	-	4	-	15	0	15
Unidentified	11	16	-	-	-	-	1	-	-	-	12	16	28
Other	2	9	-	-	1	-	2	-	9	-	14	9	23
Total	947	892	8	388	89	-	44	-	364	-	1452	1280	2732

Table 4. RMANOVA for total fish abundance. Life stage represents differences in small (< 10 cm) versus large (> 10 cm) fish. Habitat represents differences in sand, understory, and canopy habitats.

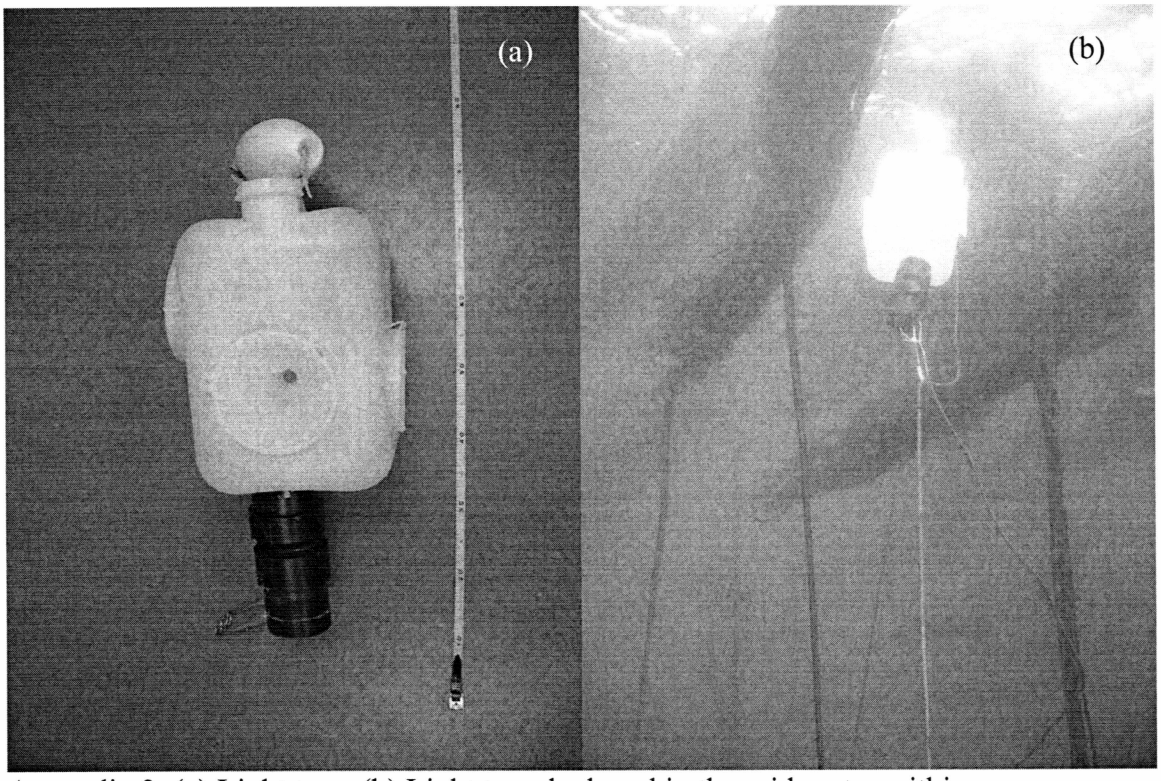
	SS	DF	MS	F	P
Life Stage	1.61	1	1.61	1.25	0.264
Family	68.11	7	9.73	7.53	<0.001
Depth of Capture	53.33	1	53.33	41.29	<0.001
Time	89.47	15	5.96	4.62	<0.001
Error	10106.21	7824	1.29		
Habitat	6.78	2	3.39	3.14	0.043
Habitat x Life Stage	38.53	2	19.27	16.25	<0.001
Error	16903.43	15648	1.08		

Table 5. RMANOVA of the four dominant fish families. Dominant families comprised at least 10% of the total abundance. Life stage represents differences in small (< 10 cm) versus large (> 10 cm) fish. Habitat represents differences in sand, understory, and canopy habitats.

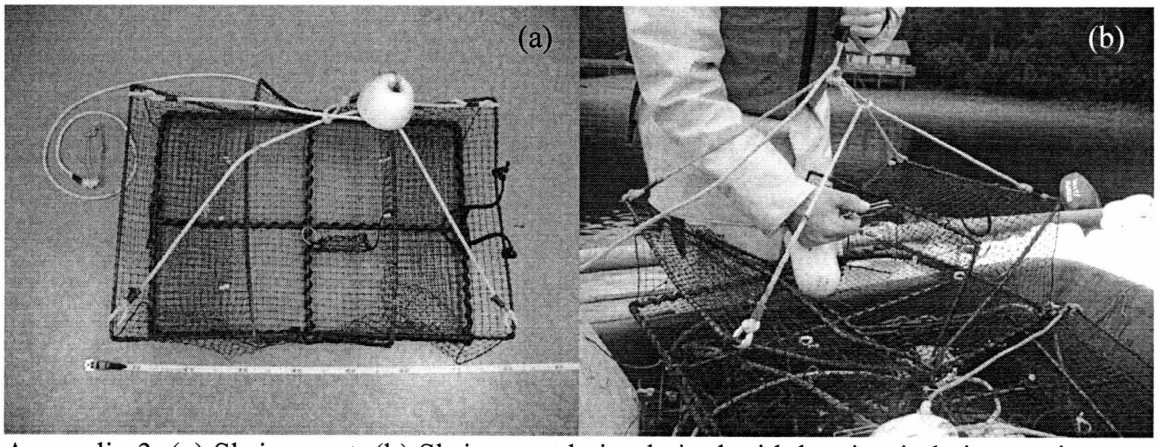
Gadidae	SS	DF	MS	F	P
Life Stage	77.39	1	77.39	14.90	<0.001
Time	249.01	15	16.60	3.20	<0.001
Error	5244.19	1010	5.19		
HABITAT	33.34	2	16.67	4.66	0.010
Error	7227.64	2020	3.58		
Pleuronectidae					
Life Stage	39.59	1	39.59	19.47	<0.001
Time	51.30	15	3.42	1.68	0.049
Error	2053.45	1010	2.03		
HABITAT	135.83	2	67.92	33.49	<0.001
Error	4096.29	2020	2.03		
Hexagrammidae					
Life Stage	52.50	1	52.50	136.54	<0.001
Time	13.98	15	0.93	2.42	0.002
Error	388.35	1010	0.38		
HABITAT	24.15	2	12.07	47.12	<0.001
Error	517.65	2020	0.26		
Sebastidae					
Life Stage	25.06	1	25.06	11.04	0.001
Time	106.39	15	7.09	3.13	<0.001
Error	2291.90	1010	2.27		
HABITAT	82.01	2	41.00	18.26	<0.001
Error	4535.39	2020	2.25		



Appendix 1. (a) Standard Monitoring Unit for the Recruitment of Fish (SMURF). (b) SMURF deployed in the mid-water within a canopy forming *Nereocystis luetkeana* bed. (c) SCUBA diver retrieving SMURF with a Benthic Ichthyofauna Net for Coral/Kelp Environments (BINCKE).



Appendix 2. (a) Light trap. (b) Light trap deployed in the mid-water within a canopy forming *Nereocystis luetkeana* bed.



Appendix 3. (a) Shrimp pot. (b) Shrimp pot being baited with herring in bait containers.

Appendix 4. Total number of species captured or observed. Fish were identified to the lowest taxonomic level possible.

Family and species name	Common Name	n	fam. total
Gadidae			796
Gadus macrocephalus	Pacific Cod	788	
Theragra chalcogramma	Walleye Pollock	8	
Pleuronectidae			517
Lepidopsetta spp.	Rock Sole	483	
Hippoglossus stenolepis	Pacific Halibut	34	
Hexagrammidae			461
Hexagrammidae spp.	Greenlings	111	
Hexagrammos decagrammus	Kelp Greenling	191	
Hexagrammos stelleri	Whitespotted Greenling	74	
Hexagrammos lagocephalus	Rock Greenling	71	
Ophiodon elongatus	lingcod	14	
Sebastidae			443
Sebastes melanops, Sebastes ciliatus	Dark Rockfish	394	
Sebastes nebulosus, Sebastes maliger, Sebastes caurinus	Banded Rockfish	49	
Cottidae			249
Cottidae spp.	Sculpins	112	
Synchirus gilli	Manacled Sculpin	68	
Hemilepidotus hemilepidotus	Red Irish Lord	34	
Blepsias cirrhosus	Silverspotted Sculpin	16	
Nautichthys oculofasciatus	Sailfin Sculpin	8	
Myoxocephalus polyacanthocephalus	Great Sculpin	6	
Hemilepidotus jordani	Yellow Irish Lord	5	
Bathymasteridae			96
Bathymaster caeruleofasciatus	Alaskan Ronquil	96	
Clupeidae			61
Clupea pallasii	Pacific Herring	61	
Stichaeidae			25
Stichaeidae spp.	Prickleback	23	
Stichaeus punctatus	Arctic Shanny	1	
Anoplarchus insignis	Slender Cockscomb	1	
Ammodytidae			18
Ammodytes hexapterus	Pacific Sand Lance	18	
Liparidae			15
Liparidae spp.	Snailfish	15	
Zaproridae			9
Zaprora silenus	Prowfish	9	
Agonidae			7
Agonidae spp.	Poachers	7	
Pholidae			5
Pholidae spp.	Gunnels	3	
Pholis laeta	Crescent Gunnel	2	
Aulorhynchidae			1
Aulorhynchus flavidus	Tubesnout	1	
Syngnathidae			1
Syngnathus leptorhynchus	Bay Pipefish	1	
Unidentified			28
Total			2732

Appendix 5. Relative abundance of fish families by habitat type over time (- indicates no fish were encountered).

			Jun 05'	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep 06'	Total
Gadidae	Sand	large (>10c	0.03	0.04	0.04	0.03	0.06	0.06	0.07	0.05	0.05	-	0.03	0.06	0.03	0.03	-	0.03	0.039
		Small (<10	0.07	0.04	0.07	-	-	-	-	-	-	-	-	-	-	-	1.22	0.31	0.106
	Understory	large (>10c	0.07	0.05	0.06	0.03	0.03	-	0.07	0.05	0.05	0.04	0.09	0.09	0.03	-	0.12	0.06	0.053
		Small (<10	0.97	1.55	1.45	0.45	0.09	-	-	-	-	-	-	-	-	0.39	0.88	0.15	0.511
	Canopy	large (>10c	-	0.12	0.15	0.03	-	-	0.12	0.05	0.10	-	-	0.06	0.06	-	-	-	0.051
		Small (<10	0.57	0.60	2.43	0.09	0.06	-	-	-	-	-	-	-	-	0.18	1.52	4.15	0.687
Pleuronectidae	Sand	large (>10c	0.47	0.05	0.16	0.12	0.15	0.03	-	-	-	-	0.03	0.06	0.42	0.22	0.06	0.03	0.113
		Small (<10	0.70	0.83	0.56	0.42	1.82	1.91	0.33	-	0.05	-	-	-	1.19	2.25	1.78	0.81	0.835
	Understory	large (>10c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Small (<10	-	-	-	0.03	-	-	-	-	-	-	-	0.03	-	-	-	-	0.004
	Canopy	large (>10c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Small (<10	-	-	-	0.03	0.03	-	-	-	-	-	-	-	-	-	-	-	0.004
Hexagrammidae	Sand	large (>10c	0.03	0.01	0.09	0.03	0.06	0.06	-	-	-	-	-	-	0.03	-	-	-	0.022
		Small (<10	-	0.03	-	-	-	-	-	-	-	-	-	0.03	-	-	0.03	0.03	0.009
	Understory	large (>10c	0.37	0.27	0.55	0.91	0.91	0.76	0.70	0.33	0.24	0.11	0.27	0.15	0.28	0.30	0.52	0.67	0.456
		Small (<10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Canopy	large (>10c	0.40	0.35	0.28	0.67	0.55	0.58	0.44	0.24	0.05	0.15	0.28	0.33	0.24	0.24	0.33	0.42	0.355
		Small (<10	-	-	-	-	-	-	-	-	-	-	-	-	-	0.06	0.06	-	0.007
Sebastidae	Sand	large (>10c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Small (<10	-	-	0.27	0.03	-	0.09	-	-	-	-	-	-	-	-	0.03	0.03	0.033
	Understory	large (>10c	0.07	0.25	0.55	1.73	0.55	0.36	-	-	-	-	-	-	0.09	0.61	3.18	3.09	0.669
		Small (<10	-	0.01	0.32	0.03	0.09	0.09	-	-	-	-	-	0.09	0.03	0.09	0.12	0.15	0.072
	Canopy	large (>10c	-	-	-	-	0.06	-	-	-	-	-	-	-	-	-	-	0.03	0.005
		Small (<10	-	0.01	0.15	0.15	0.06	0.03	-	-	-	-	-	-	-	0.06	-	-	0.033
Cottidae	Sand	large (>10c	0.37	0.05	0.04	0.06	0.06	0.09	-	-	-	0.04	0.03	0.03	0.06	0.22	0.06	0.13	0.078
		Small (<10	0.03	0.09	0.13	-	0.15	0.06	-	-	-	-	-	-	-	0.16	0.06	0.13	0.059
	Understory	large (>10c	0.17	0.12	0.04	0.12	0.21	0.15	0.22	0.10	0.19	-	-	0.03	-	-	-	0.03	0.085
		Small (<10	0.20	0.01	0.11	0.12	0.12	0.12	-	0.05	-	-	-	-	0.03	0.09	0.21	0.06	0.070
	Canopy	large (>10c	-	0.16	0.11	0.15	0.06	0.15	-	0.05	0.05	0.04	0.06	0.06	0.03	0.06	0.09	0.15	0.088
		Small (<10	-	-	0.17	0.21	0.18	0.03	0.20	-	-	-	0.03	-	0.03	0.06	0.18	0.06	0.071
Bathymasterid	Sand	large (>10c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Small (<10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Understory	large (>10c	-	-	0.26	0.24	0.21	0.21	0.26	-	-	-	0.12	0.09	0.09	0.24	0.39	0.67	0.173
		Small (<10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Canopy	large (>10c	-	-	0.02	0.03	-	-	-	-	-	-	-	-	-	-	0.09	0.03	0.011
		Small (<10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Other	Sand	large (>10c	0.03	0.01	0.04	0.03	-	-	-	-	-	0.04	-	-	0.32	0.06	0.03	1.75	0.139
		Small (<10	0.07	0.04	-	0.03	0.06	-	-	-	0.10	0.04	0.16	0.03	0.13	0.06	0.06	-	0.046
	Understory	large (>10c	-	-	-	-	0.06	0.03	0.04	-	-	-	-	-	-	-	-	-	0.007
		Small (<10	-	0.01	0.02	0.03	-	-	-	-	0.05	-	0.06	0.09	0.06	-	0.09	0.06	0.029
	Canopy	large (>10c	-	0.01	-	-	0.03	-	-	-	-	-	-	-	0.03	-	-	-	0.005
		Small (<10	-	0.01	-	0.03	-	0.12	-	-	0.05	-	0.09	0.06	0.06	-	0.12	-	0.033
Unidentified	Sand	large (>10c	0.03	0.03	-	-	-	-	-	-	-	-	-	-	-	0.16	0.03	0.06	0.020
		Small (<10	-	-	0.02	-	-	-	-	-	-	-	0.03	-	-	-	0.03	-	0.006
	Understory	large (>10c	0.03	0.01	-	-	-	-	0.04	-	-	-	-	-	0.03	-	-	-	0.007
		Small (<10	-	0.01	0.30	-	-	-	-	-	-	-	-	0.03	-	-	0.03	-	0.031
	Canopy	large (>10c	-	-	-	-	-	-	0.04	-	-	-	-	-	-	-	-	-	0.002
		Small (<10	0.03	0.01	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-	0.005